Human Population Variability in Relative Dental Development

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KEY WORDS Dental development, Population variability, Skeletal growth

ABSTRACT Using dental X-rays, the calcification of various teeth was compared between samples of black southern Africans, white French-Canadians, and prehistoric Native Americans sharing the same stage of calcification of a specified "reference tooth." The French-Canadians have markedly delayed relative development of the M_3 compared to the Africans. They also appear delayed in their M_2 development compared to both the Africans and Amerindians. While no difference in relative mandibular canine development is found between the African and French-Canadian males, French-Canadian females are advanced over the African females. Prehistoric Native Americans may be delayed in mandibular central incisor development compared to French-Canadians. These results are in general accord with other studies of variability in dental development between Africans/African Americans, Europeans/European Americans, and Native Americans, and demonstrate that population differences in ages of eruption are attributable in part to differences in relative dental development. Two potentially falsifiable hypotheses concerning the significance of population variability in relative dental development are discussed: 1) the variability (at least for molars) is associated with the amount of space in the jaws for developing teeth, 2) the variability is due to population differences in the timing of dental and skeletal development.

Recently there has been abundant debate in the paleoanthropological literature concerning the patterning and rate of dental development in fossil hominids (Beynon and Dean, 1987, 1988; Beynon and Wood, 1987; Bromage, 1987; Bromage and Dean, 1985; Conroy and Vannier, 1987, 1991; Dean, 1987a,b; Dean and Beynon, 1989; Dean et al., 1986; Mann, 1988; Mann et al., 1987, 1990, 1991; Simpson et al., 1990, 1991, 1992; Smith, 1986, 1987, 1989, 1991). One result of this debate has been the realization that we lack adequate data not only for comparing tooth development between living pongids and modern humans, but also that our knowledge of variability in dental development within and between human populations is insufficient.

Although there are many studies of population variability in eruption times of various teeth (Chagula, 1960; Debrot, 1972; Fanning, 1962; Ferguson et al., 1957; Freitas and Salzano, 1975; Garn and Moorrees, 1951; Garn et al., 1973; Hiernaux, 1968; Houpt et al., 1967; Lavelle, 1975), very few studies exist of between population variability in tooth calcification.

One approach to studying population variability in dental development involves the assessment of differences in the calcification of various teeth relative to the attained calcification status of a reference tooth. Such an approach allows one to make use of the data potentially available from skeletal samples of immature individuals of unknown ages,

Received July 18, 1993; accepted February 18, 1995.

since studies of relative dental development (as it will be referred to hereafter) do not require knowledge of actual chronological age. The only study of interpopulation differences in relative dental calcification published to date is that by Fanning and Moorrees (1969; but see also Simpson et al., 1992). They found a significant delay in calcification of mandibular third molars relative to stages of the second molar in Australian whites compared to Australian Aborigines, but found no difference between these groups in second versus first molar development.

The present study compares relative dental development in white French-Canadians, black southern Africans, and prehistoric Native Americans. Although the comparison of these three groups was undertaken as part of a study on possible differences in relative dental development between Upper Pleistocene hominids and recent humans (Tompkins, 1991), such information on recent human variability is of interest in and of itself.

MATERIALS

The French-Canadian sample was drawn from Dr. A. Demirjian's mixed longitudinal collection of dental radiographs housed at the Université de Montréal. The collection consists of panoramic dental radiographs as well as posterior-anterior and lateral cephalograms (and an occasional bitewing), although most of the data were drawn from panoramic radiographs. A total of 850 radiographs from 329 different individuals were utilized from this collection. No more than 7 radiographs from any one individual were utilized in order to reduce the amount of within-individual correlations between teeth at different stages and thereby maximize the sampling of between-individual variability. The average number of radiographs utilized per individual was 2.6 (850/329). The procedure employed was to score alternate, successive year's radiographs for each individual, skipping to a later radiograph if the reference tooth score had not changed in two years. This was done to provide comparability with the cross-sectional nature of the other two samples. (By employing this method, variability *between* individuals for a given reference tooth stage was obtained, as distinct from the variability *within* single individuals for a reference tooth stage). The youngest age scored was also varied from individual to individual so that various stages of "dental maturity" would be more evenly represented in the sample. Of the 850 scorings made on this sample, 468 were from radiographs of male children and 382 from those of female children. The age range of this sample is from 6 years to 15 years, with a mean age of 10 years.

The African sample was gathered from radiographs housed at the Dental School of the University of the Witwatersrand in Johannesburg, South Africa, the Medical University of South Africa (MEDUNSA), and from radiographs of Botswanan children taken by Mike Barter of the University of the Witwatersrand (courtesy of the Ministry of Health, Botswana). The African radiographic sample is of black children from southern Africa and includes panoramic radiographs, lateral oblique radiographs, posterior-anterior and lateral cephalograms, and an occasional bitewing. A total of 691 radiographs from 687 different individuals were utilized for this sample, 333 males and 354 females. The subjects range in age from 3 to 18 years, with a mean age of 10 years, although there are very few radiographs for the ages below 6 and above 14 years.

The Native American sample consists of periapical radiographs taken by the author on prehistoric Native American children from skeletal collections curated by the Maxwell Museum of Anthropology of the University of New Mexico, the University of Kentucky (Lexington), and the Hearst Museum of the University of California, Berkeley. The sample includes individuals from several different sites and archaeological time periods in Kentucky and surrounding states, New Mexico and bordering Southwestern states, and hunter-gatherer sites in California (see Appendix A). The total sample of radiographs comprises 520 individuals, although many, if not most, were partial dentitions due to the fragmentary nature of archaeological collections, and 201 of these could not be utilized for the recent human comparisons because the other two samples did not con-

tain individuals at comparable (i.e., early) stages of reference tooth development. No attempt was made to sex these specimens.[1]

Because chronological age is not important for this study, age estimations have not been derived for these individuals. There are relatively more Native American individuals with M1's in the early stages of root formation than Africans or French-Canadians, but relatively fewer Native Americans at later stages of M1 root development (for example see Table 1). There are also relatively fewer Native Americans available for comparisons where the M2 is used as the reference tooth (see Tables 3, 7, and 9). This accords with the fact that the Native American sample is an archaeological one, reflecting mortality patterns typical of archaeological samples.

METHODS

The teeth in each radiograph were scored as to their attained calcification stage. For the Africans and French-Canadians, only the teeth from one side of each jaw were scored (whichever side had the clearest images), unless a tooth was missing on that side or there was some obvious anomaly. In these instances, if the isomere was present and nonanomalous, then its calcification score was used. Due to the often fragmentary nature of the Native American samples scores were taken on whatever teeth were present.

The teeth were scored using a modification of the system developed by Demirjian et al. (1973). Their system divides dental calcification into eight stages for each tooth type (molars, premolars, canines and incisors). The present author added five extra stages for each tooth type which fall in between the original Demirjian stages (See Appendix B for a description of these modifications.) A replicability test for calcification stage determinations was performed on 199 uniradicular teeth (incisors, canines, and premolars) and 108 molars. This test showed that double determinations of the uniradicular teeth were exact in 81% of the cases, and the other 19% differed by one stage. In the case of molars the double determinations were exact in 91%, and the other 9% differed by one stage.

The relative development of the permanent mandibular central incisors, canines, first and second premolars, and second and third molars were compared between the three groups. The mandibular teeth were chosen because problems with image distortion are far less than with maxillary teeth. The samples were tested for differences in the frequency distributions of calcification stages of selected teeth while holding a reference tooth constant at different stages of its development. Because there were so few individuals with deciduous molars still developing in either the African or French-Canadian samples, comparisons of M1 development were not possible. Comparisons were made only where the sample size for each group was ≥ 5. The sample sizes for the Native Americans were generally smaller than for either the Africans or French-Canadians. In most cases, the Native American sample size was ≥ 10, often much larger, while the sample sizes for the other two groups were usually between 15 and 65, and most often between 20 and 50.

Pairwise, two-tailed Mann-Whitney tests corrected for ties were utilized to test for differences among the samples. These tests were performed with the "Statxact" software program (Cytel, 1989) which gives non-asymptotic, exact P-values using permutational methods. In most tests, the combined male and female samples of the Africans and French-Canadians were used (except for all canine comparisons, as noted below). In some instances only males of either of these two groups have been utilized. This was done to minimize the number of statistically significant tests resulting from very small differences between the groups being detected by very large sample sizes (where the size of any one of the combined-sex samples was ~100 or greater).

Such a multiple comparison approach increases the probability of making Type I errors among the tests. The multiple compari-

[1]Methods for estimating sex of very young individuals are generally not considered reliable (although see Schutkowski, 1993) and several of the Native American individuals were missing diagnostic portions of their pelvic remains. Thus the proportion of Native Americans which could be reliably sexed would be too small to be truly useful.

son error rate has been controlled by considering each *table* of statistical tests as a family of tests and employing the Sequential Bonferroni method (Holm, 1979; Rice, 1989) to determine whether any *P*-value is significant or not.[2]

Instead of trying to decide which reference tooth stages to utilize, and possibly missing some highly significant differences (or biasing the selective presentation of results towards those which were significant), I have chosen to present the results of tests for most of the reference tooth stages. The exceptions were those with very small sample sizes, those where the distributions of the tooth being compared fell disproportionately at either end of the range of calcification (no calcification or root completion), or those where similar information was already presented using another reference tooth (e.g., using later stages of M_1 development as references captures similar information as using early stages of M_2). Presenting the results of tests for several, successive reference tooth stages allows one to detect consistent patterns of difference (or nondifference), even if the differences do not meet the multiple comparison criteria for significance. Equally important as the results of any single statistical test is the overall patterning of the significance tests.

Within-group tests for sex differences in the French-Canadians and Africans were carried out prior to the between-group tests, as sex differences in age of attainment of calcification stages and time intervals between stages have been found in several studies (Demirjian and Levesque, 1980; Fanning, 1961; Garn et al., 1958; Levesque et al., 1981; Nolla, 1960; Tanner, 1962; Thompson et al., 1975). The only teeth showing any pattern of within-group, between-sex differences were the canines, both mandibular and maxillary (using M1 and M2 as the reference teeth). Therefore between-group comparisons of relative canine development were limited to same sex individuals, except of course for the Native American sample which contains both sexes but in unknown proportions.

The use of ranking procedures is important because, with relatively few stages of calcification for the teeth to fall into, the frequency distributions of any two groups may share the same median calcification stage, thus making it appear that the two groups do not differ in relative calcification, while in fact one of them has a significantly greater number of individuals at more advanced calcification stages than the other. Only by using the rank-ordering approach are such differences brought to light.

Tables 1–22 present the results of this study. The odd-numbered tables present the basic data used for the statistical comparisons. To make sample comparisons easier, the raw data for these tables has been transformed into percentages of individuals in each sample at the various calcification stages for a given reference tooth stage. The even-numbered tables show the *P*-values for the pair-wise Mann-Whitney tests. The *P*-values which attained table-wide significance at the multiple comparison significance level of $\alpha = 0.05$ are followed by two asterisks. The attainment of significance at the multiple comparison level of $\alpha = 0.05$ within the three tests at just one stage of reference tooth development (not tablewide) has been denoted by a single asterisk. Figures 1–13 are histograms which illustrate the degree of similarity/difference between the three samples for selected stages of reference development.

RESULTS

Tables 1 and 2 present the results of the M_2 versus M_1 comparisons. The Africans appear to be somewhat advanced in their M_2 calcification over French-Canadians for earlier stages of M_1 root development, and are significantly advanced over them for later

[2]First, the overall alpha level is set (0.05 in the present study). The *P*-values are then ranked from smallest to largest. The first (lowest) *P*-value has to meet the criterion of $P \leq \alpha/k$ where k is the number of pairwise comparisons (in the case of Table 1, k = 15). If the first *P*-value meets this criterion then it is judged as significant at the multiple comparison significance level and the next smallest *P*-value is tested using the criterion of $p \leq \alpha/(k - 1)$. If the second *P*-value meets this criterion then it is also judged as significant and the next smallest *p*-value is tested using $p \leq \alpha/(k - 2)$. This sequential testing of *P*-values continues until one of the *P*-values does not meet the criterion of $P_i \leq \alpha/(1 + k - i)$ at which time this *P*-value and all larger ones are declared nonsignificant at the multiple comparison significance level.

TABLE 1. Raw data for M_2 calcification using M_1 as the reference tooth[1]

	M_2 stages											
M_1 stage	1	2	3	4	5	6	7	8	9	10		N
			58.3	41.7								12
7	8.3	8.3	83.4									12
	4.8	19.0	50.0	26.2								42
			20.0	80.0								15
8		4.8	61.9	28.6	2.4	0.0	2.4					42
			15.4	76.9	7.7							13
			4.8	52.4	38.0	4.8						21
9		2.8	25.0	44.4	26.4	1.4						72
				31.6	63.2	5.3						19
				36.2	31.9	29.8	2.1					47
10			13.0	28.3	50.0	4.3	4.3					46
				14.3	50.0	7.1	28.6					14
				7.9	10.5	18.4	60.5	0.0	2.6		♂	38
11			1.5	4.7	53.1	14.1	26.6				♂	64
					6.5	22.5	71.0					31
						6.4	61.7	19.1	6.4	6.4	♂	47
12					16.0	10.0	62.0	12.0			♂	50
						100.0						20

[1] Quantities given are percentages of individuals at each calcification stage. Order of recent human samples is the same within each reference tooth stage; southern Africans at top, French-Canadians in the middle, Native Americans at bottom. ♂ denotes those cases where only males were used for comparisons. See discussion in text.

TABLE 2. P-values for Mann-Whitney tests on distributions of M_2 calcification relative to stages of M_1 between three recent human groups[1]

M_1 stage	Af vs. FC		Af vs. NA		FC vs. NA	
7	0.0144*	(Af)	0.0998	(Af)	0.3503	(NA)
8	0.0040*	(Af)	0.6787	(NA)	0.0024**	(NA)
9	0.0340	(Af)	0.1197	(NA)	0.0003**	(NA)
10	0.0551	(Af)	0.1283	(NA)	0.0084*	(NA)
11	0.0001[2]**	(Af)	0.4340[2]	(NA)	0.0000[2]**	(NA)
12	0.0006[2]**	(Af)	0.0280[2,3]	(Af)	0.2189[2,3]	(NA)

[1] Group in parentheses is advanced in relative dental development. Af = southern Africans; FC = French-Canadians; NA = Native Americans.
[2] Only males of Africans and French-Canadians utilized (see text).
[3] For M_1 at stage 12, all Native Americans fell into M_2 stage 7.
* Significant P-value at multiple comparison significance level of α = 0.05 for two-tailed test within a single reference tooth stage.
** Significant P-value at table-wide, multiple comparison significance level of α = 0.05 (two-tailed test).

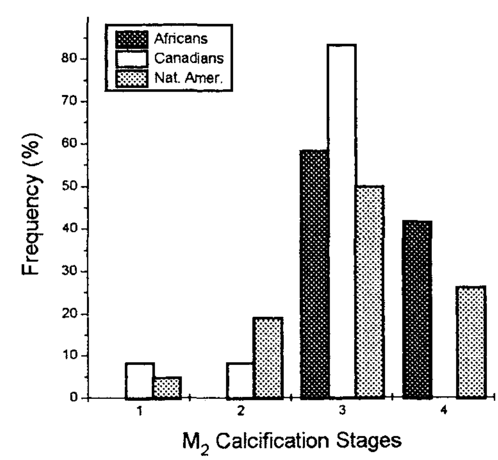

Fig. 1. Histogram of African, French-Canadian, and Native American M_2 calcification with M_1 at stage 7.

stages of M_1 development. The Native Americans are advanced over French-Canadians in three of the four middle stages tested here. While the Native American pattern of deviations from the French-Canadians is different from that of the Africans, none of the differences between the Native Americans or Africans are statistically significant. It therefore appears that the Africans and Native Americans, while not differing substantially among themselves, display varying patterns of advancement in relative dental development of the M_2 compared to the French-Canadians. Figures 1–3 show the basic trends for relative M_2 development between the samples at three different reference tooth stages.

The most striking difference between the groups is found in the M_3 comparisons presented in Tables 3–6 and Figures 4–7. The Africans are highly significantly advanced in their M_3 development compared to the French-Canadians. There is also a definite trend for them to be ahead of the Native

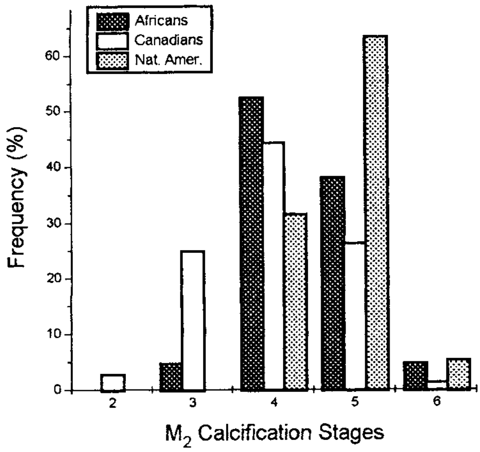

Fig. 2. Histogram of African, French-Canadian, and Native American M_2 calcification with M_1 at stage 9.

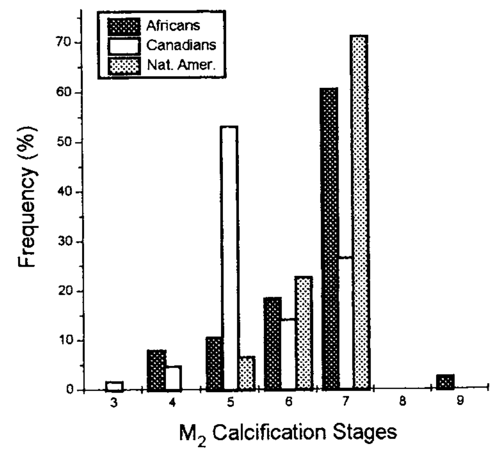

Fig. 3. Histogram of African, French-Canadian, and Native American M_2 calcification with M_1 at stage 11. Only males used for African and French-Canadian samples (see text for discussion).

Americans, especially for late stages of M_1 and earlier stages of M_2 development, although this trend only occasionally reaches tablewide significance. In addition, the data suggest that the Native Americans might be ahead of the French-Canadians for late stages of M_2 development. The degree of difference in M_3 development between the Africans and French-Canadians is the largest of all the differences found in this study.

Tables 7 and 8 and 9 and 10 present the results of group comparisons for P_3 versus M_1 and P_4 versus M_1, respectively. None of the P-values reach tablewide significance and there are no apparent trends for significant differences between any of the groups, although some of the P-values are less than 0.05. While the Africans appear consistently advanced over the French-Canadians, the differences between them are very small.

Tables 11–14 present the results of group comparisons for mandibular canine development in males and the combined-sex Native American sample. Aside from one significant difference between the Africans and French-Canadians using M_2 as the reference tooth, none of the other differences reach tablewide significance. Given that only one of the other P-values for differences between the Africans and French-Canadians attains anything close to significance, this one significant difference should probably be ignored. Thus there do not appear to be any consistent patterns of differences in these data.

Tables 15–18 present the results of group

TABLE 3. Raw data for M_3 calcification using M_1 as the reference tooth[1]

	M_3 stages									
M_1 stage	0	1	2	3	4	5	6	7		N
	50.0	37.5	12.5							40
10	93.3	6.7								45
	100.0									6
	15.6	37.5	25.0	18.8	3.1				♂	32
11	69.8	23.8	6.4						♂	63
	70.6	0.0	17.6	11.8						17
	2.3	7.0	30.2	30.2	18.6	7.0	2.3	2.3	♂	43
12	42.9	24.5	26.5	6.1					♂	49
	25.0	16.7	16.7	41.6						12

[1] See footnote in Table 1 for explanation of table organization. ♂ denotes those cases where only males were used for comparisons. See discussion in text.

TABLE 4. P-values for Mann-Whitney tests on distributions of M_3 calcification relative to stages of M_1 between three recent human groups[1]

M_1 stage	Af vs. FC	Af vs. NA	FC vs. NA
10	0.0000** (Af)	0.0446[3] (Af)	> 0.99[3] (NA)
11	0.0000[2]** (Af)	0.0070[2]** (Af)	0.6101[2] (NA)
12	0.0000[2]** (Af)	0.00137[2]* (Af)	0.0536[2] (NA)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
[2] Only males of Africans and French-Canadians utilized (see text).
[3] For M_1 at stage 10, all Native Americans fell into M_3 stage 0.
* Significant P-value at multiple comparison significance level of α = 0.05 for two-tailed test within a single reference tooth stage.
** Significant P-value at table-wide, multiple comparison significance level of α = 0.05 (two-tailed test).

TABLE 6. P-values for Mann-Whitney tests on distributions of M_3 calcification relative to stages of M_2 between three recent human groups[1]

M_2 stage	Af vs. FC	Af vs. NA	FC vs. NA
7	0.0000** (Af)	0.0002** (Af)	0.5333 (NA)
8	0.0000** (Af)	0.0118* (Af)	0.1295 (NA)
9	0.0000** (Af)	0.0085* (Af)	0.8038 (NA)
10	0.0000** (Af)	0.0630 (Af)	0.0343 (NA)
11	0.0000** (Af)	0.0607 (Af)	0.0192* (NA)
12	0.0000** (Af)	0.0552 (Af)	0.0155* (NA)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development. Only males of Africans and French-Canadians utilized (see text).
* Significant P-value at multiple comparison significance level of α = 0.05 for two-tailed test within a single reference tooth stage.
** Significant P-value at table-wide, multiple comparison significance level of α = 0.05 (two-tailed test).

comparisons for mandibular canine development in females and the combined-sex Native American sample. Using M_1 as the reference tooth (which samples earlier stages of canine development) the only significant differences appear to exist between the French-Canadians and Native Americans, the former being advanced in their canine development at earlier stages of M_1 (see Table 15, M_1 stages 8 and 9). Using M_2 as the reference tooth (which samples later stages of canine development) the French-Canadians are consistently highly advanced over the Native Americans (see Table 17). The French-Canadian females are also advanced over the Africans females. There is a trend for the Africans to be ahead of the Native Americans, but none of these differences reach tablewide significance. Figures 8–10 show the basic trends between the samples for three stages of M_2 calcification.

One could argue that the apparent advancement of the French-Canadian females over their African counterparts might be due, at least in part, to the relative advancement of M_2 calcification in the Africans. If there were in fact no differences between the two groups of females in canine development, the advanced M_2 calcification of the African females would make their canine development appear delayed relative to the M_2. Yet this difference in relative M_2 development should result in a pattern of significant

TABLE 5. Raw data for M_3 calcification using M_2 as the reference tooth[1]

M_2 stage	M_3 stages 0	1	2	3	4	5	6	7	8	9		N
	3.2	14.3	34.9	36.5	11.1						♂	63
7	36.8	27.6	30.3	5.3							♂	76
	45.2	9.7	16.1	29.0								31
			9.5	33.3	47.6	4.8	0.0	4.8			♂	21
8	9.1	16.4	34.5	34.5	5.5						♂	55
			28.6	71.4								7
				15.0	25.0	45.0	10.0	5.0			♂	20
9	8.8	2.9	11.8	35.3	32.4	8.8					♂	34
	8.3	8.3	16.7	16.7	33.3	8.3	8.3					12
				8.8	38.2	5.9	5.9	41.2			♂	34
10	6.3	3.1	6.2	40.6	31.3	9.4	3.1				♂	32
			7.1	28.6	14.3	28.6	14.3	7.1				14
					5.7	17.0	11.3	58.5	7.5		♂	53
11				10.3	41.0	23.0	5.1	15.4	2.6	2.6	♂	39
				6.3	6.3	31.2	18.7	31.2	6.3			16
					5.6	0.0	0.0	72.2	22.2		♂	18
12			2.2	2.2	17.8	31.1	8.9	35.6	0.0	2.2	♂	45
						14.3	21.4	57.1	7.2			14

[1] See footnote in Table 1 for explanation of table organization. ♂ denotes those cases where only males were used for comparisons. See discussion in text.

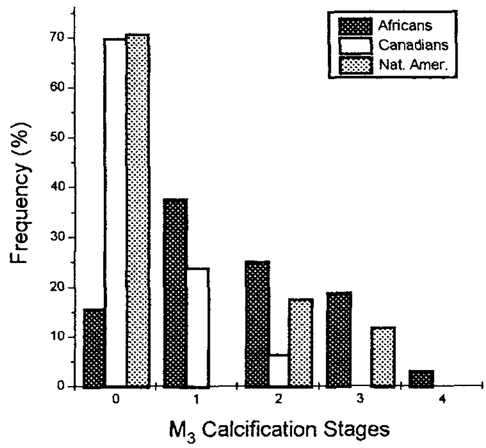

Fig. 4. Histogram of African, French-Canadian, and Native American M_3 calcification with M_1 at stage 11. Only males used for African and French-Canadian samples (see text for discussion).

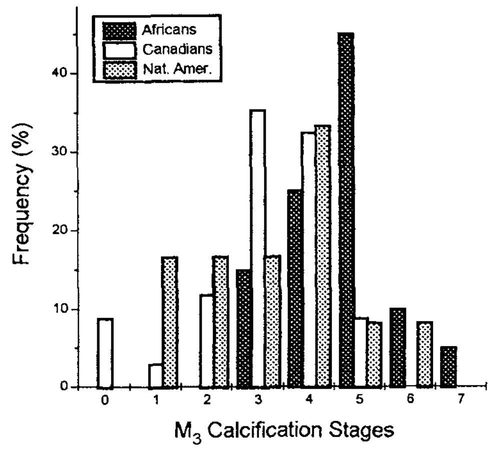

Fig. 6. Histogram of African, French-Canadian, and Native American M_3 calcification with M_2 at stage 9. Only males used for African and French-Canadian samples (see text for discussion).

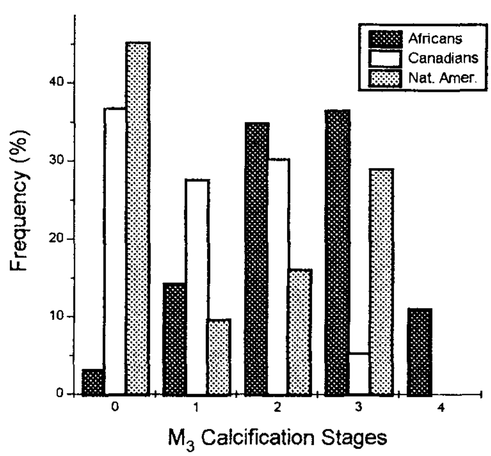

Fig. 5. Histogram of African, French-Canadian, and Native American M_3 calcification with M_2 at stage 7. Only males used for African and French-Canadian samples (see text for discussion).

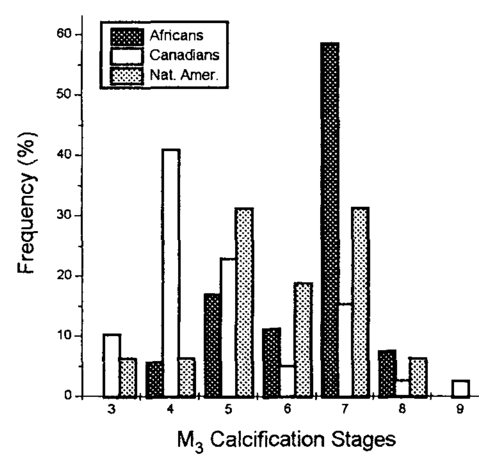

Fig. 7. Histogram of African, French-Canadian, and Native American M_3 calcification with M_2 at stage 11. Only males used for African and French-Canadian samples (see text for discussion).

canine differences between the African and French-Canadian males in Table 14, given the lack of within-population sex differences in relative M_2 development, but none is found. In addition, when female canine development is compared using P_4 as the reference tooth (see Tables 19, 20, and Figure 11) a similar pattern of French-Canadian advancement is found, although the *P*-values are generally lower and do not attain tablewide significance as often as when using the M_2. Thus the difference in M_2 relative development between the French-Canadians and Africans might account for some of the female difference in relative canine development but certainly not all of it.

The unknown representation of the sexes in the Native American sample makes it difficult to interpret the results of comparisons with the other two groups, especially

TABLE 7. Raw data for P_3 calcification using M_1 as the reference tooth[1]

	P_3 stages											
M_1 stage	3	4	5	6	7	8	9	10	11	12		N
		33.3	66.7									15
8	3.0	42.4	27.3	9.1	18.2							33
		38.5	53.8	7.7								13
		4.8	61.9	28.6	4.8							21
9		4.8	46.8	6.5	41.9							62
		15.0	35.0	30.0	20.0							20
			37.8	26.7	35.5							45
10			25.0	6.8	61.4	6.8						44
			7.1	42.9	50.0							14
			10.3	5.1	53.8	17.9	12.8				♂	39
11			7.8	3.1	76.6	7.8	4.7				♂	64
				6.9	75.9	6.9	10.3					29
					41.3	28.3	17.4	4.3	6.5	2.2	♂	46
12					34.0	42.0	22.0	0.0	2.0		♂	50
					31.6	47.4	10.5	10.5				19

[1] See footnote in Table 1 for explanation of table organization. ♂ denotes those cases where only males were used for comparisons. See discussion in text.

TABLE 8. P-values for Mann-Whitney tests on distributions of P_3 calcification relative to stages of M_1 between three recent human groups[1]

M_1 stage	Af vs. FC	Af vs. NA	FC vs. NA
8	0.7694 (Af)	> 0.99 (Af)	0.7489 (NA)
9	0.0528 (FC)	0.4343 (NA)	0.3086 (FC)
10	0.0062* (FC)	0.0986 (NA)	0.4771 (FC)
11	0.1961[2] (Af)	0.7633[2] (Af)	0.3690[2] (NA)
12	0.9170[2] (Af)	0.9576[2] (NA)	0.8893[2] (NA)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
[2] Only males of Africans and French-Canadians utilized (see text).
* Significant P-value at multiple comparison significance level of α = 0.05 for two-tailed test within a single reference tooth stage.

the highly significant differences from the French-Canadian females. However, the marked difference between the French-Canadian females and the mixed-sex Native Americans and the lack of reversal in this pattern when the French-Canadian males are compared to the Native Americans suggests that the French-Canadian females are probably advanced over female Native Americans.

Tables 21 and 22 present the results of I_1 comparisons between the groups. The results are rather inconsistent and therefore difficult to interpret in any broad sense. The only significant difference between the Afri-

TABLE 9. Raw data for P_4 calcification using M_1 as the reference tooth[1]

	P_4 stages												
M_1 stage	0	1	2	3	4	5	6	7	8	9	10	11		N
			6.7	6.7	73.3	13.3								15
8	3.0	0.0	6.1	33.3	48.5	9.1								33
		7.7	0.0	23.1	61.5	7.7								13
					28.6	61.9	9.5							21
9		1.8	3.5	3.5	40.4	43.9	1.7	5.2						57
				18.8	43.7	31.2	6.3							16
					10.9	50.0	26.1	13.0						46
10		4.4	2.2	2.2	20.0	42.2	9.0	20.0						45
				14.3	21.4	21.4	28.6	14.3						14
					5.1	12.8	5.2	61.5	15.4				♂	39
11				1.6	3.2	20.6	7.9	65.1	1.6				♂	63
				3.3	0.0	3.3	30.0	56.7	6.7					30
						2.2	4.3	54.3	19.6	8.7	8.7	2.2	♂	46
12		2.0	0.0	0.0	2.0	4.0	2.0	62.0	16.0	12.0			♂	50
								57.1	28.6	14.3				21

[1] See footnote in Table 1 for explanation of table organization. ♂ denotes those cases where only males were used for comparisons. See discussion in text.

TABLE 10. P-values for Mann-Whitney tests on distributions of P_4 calcification relative to stages of M_1 between three recent human groups[1]

M_1 stage	Af vs. FC	Af vs. NA	FC vs. NA
8	0.0985 (Af)	0.2862 (Af)	0.6143 (NA)
9	0.1020 (Af)	0.0321 (Af)	0.3031 (FC)
10	0.1396 (Af)	0.4300 (Af)	0.9792 (NA)
11	0.0621[2] (Af)	0.2793[2] (Af)	0.5589[2] (NA)
12	0.2116[2] (Af)	0.8286[2] (Af)	0.1853[2] (NA)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
[2] Only males of Africans and French-Canadians utilized (see text).

TABLE 12. P-values for Mann-Whitney tests on distributions of $\overline{C}$ calcification relative to stages of M_1 between male Africans and French-Canadians and a mixed-sex Native American sample[1]

M_1 stage	Af vs. FC	Af vs. NA	FC vs. NA
8	0.5607 (FC)	0.5818 (NA)	0.9142 (FC)
9	0.3902 (FC)	0.4480 (Af)	0.0106* (FC)
10	0.5748 (FC)	> 0.99 (Af)	0.6332 (FC)
11	0.1413 (Af)	0.6464 (NA)	0.0241 (NA)
12	0.8413 (FC)	0.1002 (NA)	0.0170 (NA)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
* Significant P-value at multiple comparison significance level of α = 0.05 for two-tailed test within a single reference tooth stage.

cans and French-Canadians appears near the end of M_1 root development (see Table 21, stage 12) with French-Canadians advancing over the Africans. The fact that French-Canadians are also significantly advanced over the Native Americans for M_1 stage 12 suggests that advancement of the I_1 near the end of its development might be characteristic of this population. The low P-values for M_1 stages 8 and 9 in the comparisons of the French-Canadians and Native Americans (see Table 22) are mirrored in the low P-values at these same M_1 stages for the comparisons of the Africans and Native Americans. In both cases, the Native Americans are delayed in their I_1 calcification (see Fig. 12). Overall, it is probably best to consider the results of the incisor comparisons as indicating no pattern of differences, except an inconsistent pattern of delayed incisor development in the Native Americans.

As a check against the possibility that some of the differences between the recent human samples were due in part to the use of a mixed longitudinal sample for the French-Canadians while the other two samples were cross-sectional, a few alternate statistical comparisons were performed. Tests for differences in M_3 development between the French-Canadians versus the southern Africans and Native Americans were redone for M_2 stages 7 and 9, eliminating any French-Canadian individuals from the samples for M_2 stages 7 and 9 which were used for the tests at M_2 stage 8. Thus the French-Canadian samples used for the M_3 tests at these three M_2 stages consisted of entirely different individuals, as did the southern African and Native American samples. In each case the differences between the southern Africans and French-Canadians remained

TABLE 11. Raw data for $\overline{C}$ calcification in male Africans and French-Canadians and a mixed-sex Native American sample using M_1 as the reference tooth[1]

	$\overline{C}$ stages									
M_1 stage	4	5	6	7	8	9	10	11	12	N
	28.6	28.6	14.2	28.6						7
8	10.6	36.8	15.8	36.8						19
		33.3	58.4	8.3						12
		30.0	10.0	60.0						10
9		16.3	11.6	72.1						43
		21.1	47.3	31.6						19
		19.3	3.8	73.1	3.8					26
10		15.0	0.0	80.0	5.0					20
		7.7	15.4	76.9						13
		3.0	6.1	57.6	18.2	9.1	3.0	3.0		33
11		3.2	3.2	77.8	9.5	6.3				63
			3.6	57.1	28.6	10.7				28
		2.2	0.0	37.8	26.7	11.1	8.9	13.3		45
12				26.5	42.9	24.5	6.1			49
				21.0	15.8	26.3	31.6	5.3		19

[1] See footnote in Table 1 for explanation of table organization.

TABLE 13. Raw data for $\overline{C}$ calcification in male Africans and French-Canadians and a mixed-sex Native American sample using M_2 as the reference tooth[1]

	$\overline{C}$ stages							
M_2 stage	7	8	9	10	11	12	13	N
	47.0	33.3	10.6	4.5	4.5			66
7	22.6	34.7	34.7	5.3	2.7			75
	36.2	27.6	22.4	12.1	1.7			58
	6.5	6.5	25.8	29.0	29.0	3.2		31
8	3.8	1.9	30.8	40.4	17.3	1.9	3.8	52
		33.3	33.3	33.3				6
		4.2	12.5	16.7	45.8	12.5	8.3	24
9			11.8	14.7	58.8	5.9	8.8	34
			9.1	54.5	36.4			11
			5.7	0.0	60.0	22.9	11.4	35
10			6.5	16.1	51.6	9.7	16.1	31
					41.7	41.7	16.6	12
					25.5	46.8	27.7	47
11				2.6	23.7	13.2	60.5	38
					23.1	23.1	53.8	13

[1] See footnote in Table 1 for explanation of table organization.

TABLE 14. P-values for Mann-Whitney tests on distributions of $\overline{C}$ calcification relative to stages of M_2 between male Africans and French-Canadians and a mixed-sex Native American sample[1]

M_2 stage	Af vs. FC	Af vs. NA	FC vs. NA
7	0.0015** (FC)	0.0983 (Af)	0.3040 (FC)
8	0.9658 (FC)	0.1112 (Af)	0.0596 (FC)
9	0.8453 (FC)	0.1433 (Af)	0.0421 (FC)
10	0.2358 (Af)	0.1546 (NA)	0.0498 (NA)
11	0.0512 (FC)	0.2306 (NA)	0.8830 (FC)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
** Significant P-value at table-wide, multiple comparison significance level of $\alpha = 0.05$ (two-tailed).

highly statistically significant, and the direction of differences remained the same.[3] Thus it does not appear that the results of this study were affected to any significant degree by comparing cross-sectional samples with a mixed longitudinal one.

In summary, the statistical comparisons presented here show that

1) the Africans and Native Americans are advanced in relative M_2 calcification compared to the French-Canadians, but not consistently so, and their patterns of advancement over French-Canadians contrast with one another;

2) the Africans are markedly and consistently advanced in the relative calcification of their M_3 compared to the French-Canadians, and are also advanced over the Native Americans, but to a lesser degree. The data suggest that the Native Americans are advanced over the French-Canadians for later stages of M_3 development (where they differ the least from the Africans). Thus the approximate order of M_3 advancement between the groups is Africans > Native Americans > French-Canadians;

3) no differences exist between the groups in their relative premolar calcification;

4) the French-Canadian females are advanced over the African females in their mandibular canine calcification, although not consistently so, and are probably advanced over their Native American counterparts, although the mixed-sex Native American sample renders such comparisons difficult to interpret;

5) no consistent pattern of significant differences in mandibular canine calcification exists between the African and French-Canadian males or the mixed-sex Native American sample; and

6) there is an inconsistent pattern of delay

[3] At M_2 stage 7 the P-value for the advancement of the Africans over the reduced French-Canadian sample ($n = 50$) remained at $P = 0.0000$, while the difference between the French-Canadians and Native Americans remained non-significant at $P = 0.6659$. At M_2 stage 9 the P-value for the advancement of the Africans over the reduced French-Canadian sample ($n = 10$) was $P = 0.0009$, still highly significant at the table-wide, multiple comparison significance level of $\alpha = 0.05$. The difference between the Native Americans and French-Canadians remained non-significant at $P = 0.6546$.

TABLE 15. Raw data for $\overline{C}$ calcification in female Africans and French-Canadians and a mixed-sex Native American sample using M_1 as the reference tooth[1]

	$\overline{C}$ stages								
M_1 stage	5	6	7	8	9	10	11	12	N
	40.0	0.0	60.0						5
8	12.5	6.3	81.2						16
	33.3	58.3	8.3						12
		40.0	60.0						5
9		5.3	84.2	10.5					19
	21.0	47.4	31.6						19
			100.0						13
10		4.0	72.0	20.0	4.0				25
	7.7	15.4	76.9						13
			44.4	35.2	14.8	5.6			54
11			42.2	37.8	15.6	2.2	2.2		45
		3.6	57.1	28.6	10.7				28
			17.1	22.9	37.1	8.6	11.4	2.9	35
12			16.7	22.2	27.8	30.6	2.7		36
			21.0	15.8	26.3	31.6	5.3		19

[1] See footnote in Table 1 for explanation of table organization.

TABLE 16. P-values for Mann-Whitney tests on distributions of $\overline{C}$ calcification relative to stages of M_1 between female Africans and French-Canadians and a mixed-sex Native American sample[1]

M_1 stage	Af vs. FC	Af vs. NA	FC vs. NA
8	0.4427 (FC)	0.4173 (Af)	0.0005** (FC)
9	0.0961 (FC)	0.2953 (Af)	0.0000** (FC)
10	0.1323 (FC)	0.2200[2] (Af)	0.0125 (FC)
11	0.8950 (FC)	0.1019 (Af)	0.0882 (FC)
12	0.8306 (FC)	0.7895 (NA)	0.9030 (NA)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
[2] For M_1 at stage 10, all Africans fell into $\overline{C}$ stage 7.
** Significant P-value at table-wide, multiple comparison significance level of $\alpha = 0.05$ (two-tailed).

in I_1 development in the Native Americans compared to the other two groups.

DISCUSSION

Significance of the results with regard to other studies on dental maturation

Population variability in eruption. There is extensive documentation of differences in age of attainment of dental maturation markers, mostly tooth eruption, between various modern populations. Those studies comparing African-derived versus European-derived populations are of particular interest to the present research.

TABLE 17. Raw data for $\overline{C}$ calcification in female Africans and French-Canadians and a mixed-sex Native American sample using M_2 as the reference tooth[1]

	$\overline{C}$ stages							
M_2 stage	7	8	9	10	11	12	13	N
	22.2	34.6	24.7	12.3	6.2			81
7	3.3	18.0	34.4	29.5	13.1	1.6		61
	36.2	27.6	22.4	12.1	1.7			58
		6.5	29.0	19.4	29.0	16.1		31
8			15.1	30.3	42.4	6.1	6.1	33
		33.3	33.3	33.3				6
			5.3	15.8	57.9	10.5	10.5	19
9				4.5	36.4	13.6	45.5	22
			9.1	54.5	36.4			11
					21.2	27.3	51.5	33
10					6.9	13.8	79.3	29
					41.7	41.7	16.6	12
					10.9	29.7	59.4	64
11					2.3	0.0	97.7	44
					23.1	23.1	53.8	13

[1] See footnote in Table 1 for explanation of table organization.

TABLE 18. P-values for Mann-Whitney tests on distributions of $\overline{C}$ calcification relative to stages of M_2 between female Africans and French-Canadians and a mixed-sex Native American sample[1]

M_2 stage	Af vs. FC	Af vs. NA	FC vs. NA
7	0.0000** (FC)	0.1278 (Af)	0.0000** (FC)
8	0.2628 (FC)	0.0401 (Af)	0.0014** (FC)
9	0.0059** (FC)	0.0185* (Af)	0.0008** (FC)
10	0.0245* (FC)	0.0474* (Af)	0.0000** (FC)
11	0.0000** (FC)	0.5777 (Af)	0.0003** (FC)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
* Significant P-value at multiple comparison significance level of α = 0.05 for two-tailed test within a single reference tooth stage.
** Significant P-value at table-wide, multiple comparison significance level of α = 0.05 (two-tailed).

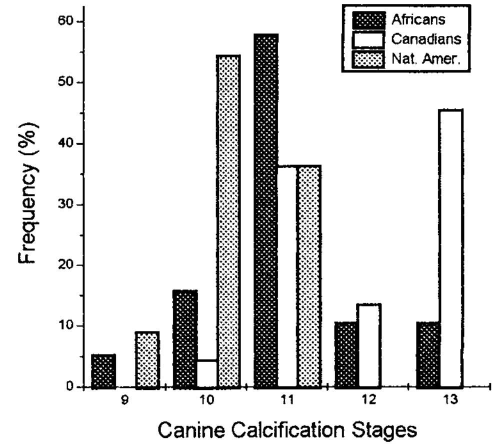

Fig. 9. Histogram of female African, female French-Canadian, and mixed-sex Native American mandibular canine calcification with M_2 at stage 9.

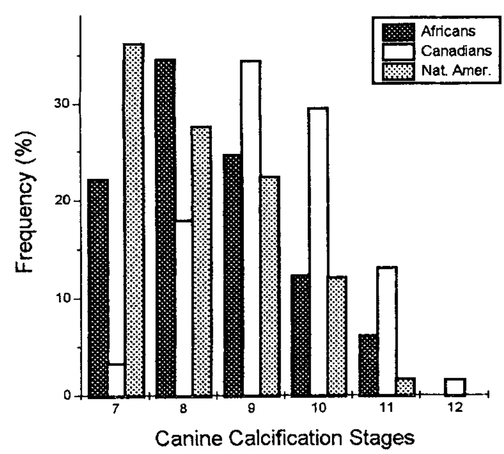

Fig. 8. Histogram of female African, female French-Canadian, and mixed-sex Native American mandibular canine calcification with M_2 at stage 7.

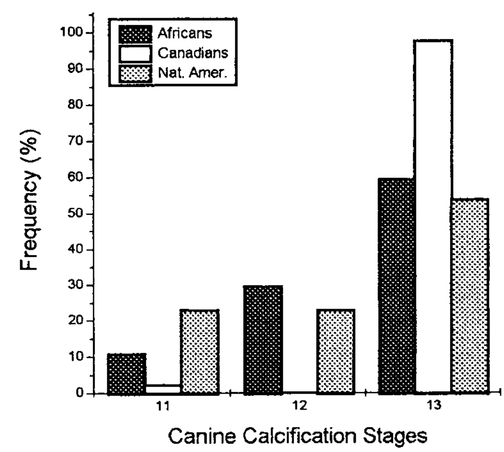

Fig. 10. Histogram of female African, female French-Canadian, and mixed-sex Native American mandibular canine calcification with M_2 at stage 11.

Garn et al. (1973) found significant advancement in low-income African-Americans compared to low-income European-Americans in age of emergence of permanent teeth. The greatest differences were in the permanent incisors followed by the molars, with the smallest differences in the premolars and canines. Ferguson et al. (1957) found that African-Americans erupt their first deciduous tooth earlier than European-Americans. However, middle socioeconomic level European-Americans have more teeth erupted, on average, than African-Americans from lower socioeconomic levels at one year of age. Houpt et al. (1967), comparing African children from Ghana to European-Americans, found that Ghanans erupt their teeth earlier. Debrot (1972), Freitas and Salzano (1975), Hassanali (1985), Hassanali and Odhiambo (1981), Hiernaux (1968), and Lavelle (1975) have also found similar advancement of eruption in their respective samples of African- and European-derived children in different parts of the world.

The review of interpopulation differences in growth and development by Eveleth and Tanner (1976, 1990) shows the advancement

TABLE 19. Raw data for $\overline{C}$ calcification in female Africans and French-Canadians and a mixed-sex Native American sample using P_4 as the reference tooth[1]

P_4 stage	$\overline{C}$ stages 7	8	9	10	11	12	13	N
	42.6	37.7	9.8	6.6	3.3			61
7	22.4	28.4	28.4	16.4	4.5			67
	42.1	34.2	15.8	7.9				38
		14.3	48.6	22.9	14.3			35
8		10.3	27.6	41.4	17.2	3.5		29
		14.3	50.0	28.6	7.1			14
		10.3	23.0	12.8	35.9	15.4	2.6	39
9			16.7	16.7	40.0	0.0	26.6	30
		7.7	15.4	46.1	23.1	7.7		13
			4.1	12.5	29.2	29.2	25.0	24
10					32.0	8.0	60.0	25
			10.0	30.0	40.0	20.0		10
					19.2	34.0	46.8	47
11				2.4	9.5	7.1	80.9	42
					44.4	11.2	44.4	9
					11.1	18.5	70.4	27
12						8.3	91.7	12
						66.7	33.3	9

[1] See footnote in Table 1 for explanation of table organization.

TABLE 20. P-values for Mann-Whitney tests on distributions of $\overline{C}$ calcification relative to stages of P_4 between female Africans and French-Canadians and a mixed-sex Native American sample[1]

P_4 stage	Af vs. FC	Af vs. NA	FC vs. NA
7	0.0010** (FC)	0.8845 (NA)	0.0057* (FC)
8	0.0988 (FC)	0.8662 (Af)	0.1206 (FC)
9	0.0735 (FC)	0.5047 (Af)	0.0521 (FC)
10	0.0278 (FC)	0.0397 (Af)	0.0001** (FC)
11	0.0033** (FC)	0.4928 (Af)	0.0205* (FC)
12	0.1856 (FC)	0.1154 (Af)	0.0158* (FC)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
* Significant P-value at multiple comparison significance level of α = 0.05 for two-tailed test within a single reference tooth stage.
** Significant P-value at table-wide, multiple comparison significance level of α = 0.05 (two-tailed).

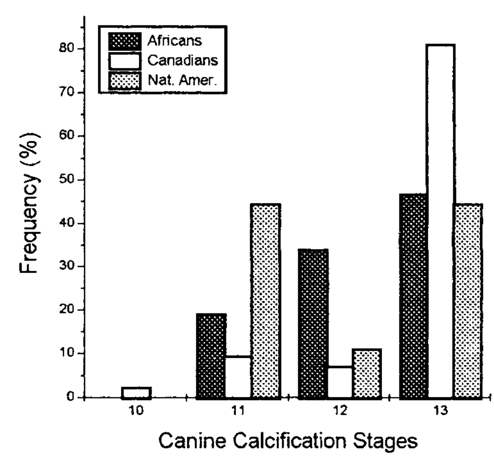

Fig. 11. Histogram of female African, female French-Canadian, and mixed-sex Native American mandibular canine calcification with P_4 at stage 11.

of at least some African groups over European and Asian populations in the mean age of eruption of the maxillary and mandibular M1's and M2's, although New Guineans often match their advancement. (However, the data they present shows that African-Americans have either similar or delayed ages of eruption for these teeth.) Data on median age at eruption of the permanent maxillary second molars in Hiernaux (1968) indicates that Africans erupt these teeth earlier than European-Americans. Concerning third molars in particular, Chagula (1960) and Fanning (1962) found that the percentage of East African males with erupted third molars was significantly greater than the percentage of White Bostonians for any given age. Hassanali (1985) confirms this earlier third molar eruption and also shows that Kenyan Africans are advanced over Kenyan Asiatics.

There are fewer studies which compare Native Americans with other populations. Garn and Moorrees (1951) found that Aleuts were advanced in age of emergence of permanent teeth over standards of mean age of emergence for European-Americans. Steg-

TABLE 21. Raw data for I_1 calcification using M_1 as the reference tooth[1]

	I_1 stages									
M_1 stage	5	6	7	8	9	10	11	12	13	N
	10.0	10.0	60.0	20.0						10
7	10.0	20.0	70.0							10
		21.3	78.7							47
			33.3	25.0	41.7					12
8	3.5	0.0	44.8	31.0	10.3	0.0	10.4			29
			92.3	0.0	7.7					13
			13.3	6.7	40.0	0.0	40.0			15
9			5.7	17.0	24.5	9.4	37.7	1.9	3.8	53
			50.0	21.4	21.4	0.0	7.2			14
				2.8	27.8	16.6	50.0	0.0	2.8	36
10			2.6	5.1	20.5	7.7	56.4	5.1	2.6	39
			16.7	0.0	16.7	50.0	16.7			6
				1.6	4.8	1.6	38.1	31.7	22.2	63
11					7.8	0.0	45.1	9.8	37.3	51
						4.3	21.7	52.2	21.7	23
							13.0	25.9	61.1	54
12							3.8	3.8	92.4	53
							13.3	46.7	40.0	15

[1] See footnote in Table 1 for explanation of table organization.

TABLE 22. P-values for Mann-Whitney tests on distributions of I_1 calcification relative to stages of M_1 between three recent human groups[1]

M_1 stage	Af vs. FC		Af vs. NA	FC vs. NA	
7	0.4319	(Af)	0.3316 (Af)	0.4846	(NA)
8	0.3315	(Af)	0.0061*(Af)	0.0225*	(FC)
9	0.5866	(FC)	0.0057*(Af)	0.0001**	(FC)
10	0.4447	(FC)	0.2203 (Af)	0.0962	(FC)
11	0.7472	(FC)	0.2504 (NA)	0.4823	(NA)
12	0.0002**	(FC)	0.2692 (Af)	0.0000**	(FC)

[1] See Table 2 for explanation of symbols identifying which recent human group was advanced in relative dental development.
* Significant P-value at multiple comparison significance level of $\alpha = 0.05$ for two-tailed test within a single reference tooth stage.
** Significant P-value at table-wide, multiple comparison significance level of $\alpha = 0.05$ (two-tailed).

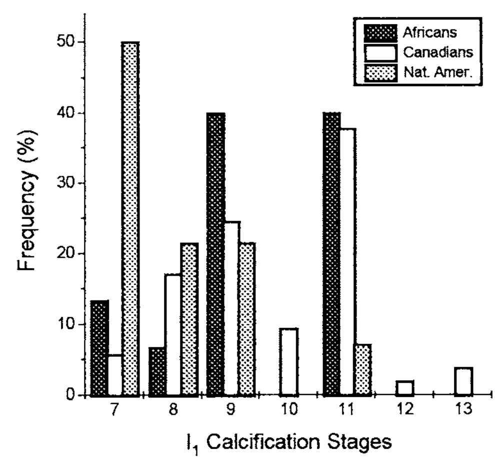

Fig. 12. Histogram of African, French-Canadian, and Native American I_1 calcification with M_1 at stage 9.

gerda and Hill (1942) found differences in mean age of eruption between four different populations, with their Navajo sample being advanced over both African- and European-Americans. However, this study has been criticized for its statistical methodology (Dahlberg and Menegaz-Bock, 1958; Smith, 1991). Dahlberg and Menegaz-Bock (1958), using appropriate statistical approaches, found that the anterior permanent dentition of Pima Native Americans erupted at later ages than English children, while their posterior permanent teeth (through the M2) erupted earlier. The results of this latter study seem to correspond with the general pattern found in the present research; compared to French-Canadians, Native Americans are somewhat advanced in relative development of the permanent M_2 and M_3, but possibly delayed in their relative incisor and canine calcification.

The results of the present study indicate that differences between the above-discussed African-derived, European-derived, and Native American samples in dental eruption (and probably calcification schedules; see below) are attributable in part to differing patterns of relative development between certain teeth. For example, either 1) French-Canadians have rates of calcification

of the M_1, M_2, and M_3 similar to those of the Africans but have longer time periods between initiation of calcification of these teeth; or 2) they have *average* rates of M_2 and M_3 calcification which are slower than that of the M_1 compared to the Africans, with time periods between initiation of calcification similar to the Africans; or 3) they are characterized by a combination of both these patterns. Given the consistent pattern of delay in M_3 and, to a lesser extent, M_2 calcification shown by the French-Canadians from the earliest stages of calcification onwards (see Tables 3 and 4 and Fig. 13, discussed below), the first hypothesis is the most likely.

Population variability in tooth calcification. The only study to date which has compared tooth mineralization standards for African- and European-derived children is that recently published by Harris and McKee (1990). They found that African-Americans from the U.S. midsouth were advanced for all teeth in age of attainment of tooth calcification stages compared to midsouth European-Americans. Comparing their data to those of Anderson et al. (1976) for Ontario European-Americans, they found that the Canadians were advanced in age of attainment over midsouth European-Americans. They interpret this as showing regional differences in both environmental and genetic components for the rate of dental calcification.

A study by Loevy (1983) applied to Demirjian et al. (1973) method for assessing dental maturity to samples of latino, African-American, and European-American children. Loevy compared the distributions of maturity scores (based on combined calcification scores for seven permanent mandibular teeth in one quadrant) for given chronological ages between same-sex categories of his three samples. He found that African-Americans had significantly more advanced maturity scores than their European-American counterparts. Importantly, he found that all of his samples were advanced in the distributions of their maturity scores over the French-Canadian sample Demirjian et al. (1973) used. Sapoka and Demirjian (1971) have stated that French-Canadians appear to have somewhat slower dental maturation than other North American children. Since the present study is based on the same French-Canadian collection, the degree of differences in the present study between the French-Canadians and the Africans and Native Americans may be more extreme than one would find using another European-American sample.

Chertkow (1980) found that South African black children were advanced in dental calcification over white South Africans when children of both populations exhibiting the earliest stage of pollical adductor sesamoid calcification were compared. However, it is possible that Chertkow's sample of black children may not be dentally advanced for their actual age, but only relative to beginning ossification of their pollical adductor sesamoid, which is probably delayed compared to the white children. The mean skeletal age of the black children (using the T.W.2 method of Tanner et al., 1975) was, on average, about 1 year behind their mean chronological age, while the match between mean skeletal and chronological ages for the white children was nearly perfect.

Owsley and Jantz (1983), applying the dental calcification standards of Moorrees et al. (1963) to immature individuals from the Arikara skeletal collection, concluded that there were population differences in tooth-formation timing between the Arikara and American whites. In particular they found a significant difference between the ages assigned for first and second premolars and those assigned for M3 development, with the M3 age assignments being advanced by more than 2 years over the premolar ages. They also found that the ages assigned to maxillary incisors and mandibular M2's were advanced by 0.5 to 1.1 years over the premolar ages. These results are in general accord with those of the present study, in that they indicate advancement in relative development of the M_3 and (to a lesser extent) M_2 in Native Americans.

It is obvious from the present study that the claim by Simpson et al. that "... population differences are not a major source of variation in human dental development" (1992, p. 33) is incorrect. In order to determine whether any population differences exist in relative dental calcification,

Simpson and his coworkers (1992) compared the Hamann-Todd collection of European- and African-Americans to their Libben Native American sample. Both the relatively small sample sizes and the questionable statistical approach used in their study (see Anemone and Watts, 1992) are undoubtedly the reasons for the discrepancies between their conclusions and those of the present author. The mixed population nature of the Hamann-Todd collection also probably contributed to this erroneous conclusion. Given the results of the present study and the fairly extensive literature on population differences in various aspects of dental development cited above, their rather broad, sweeping statement simply cannot be supported.

Hypotheses concerning population variability in relative dental development

Two general hypotheses regarding the significance of population variability in relative dental development, in particular relative M3 and M2 development, can be put forward. These hypotheses are based on data and ideas presented by various researchers. The first posits a relationship between tooth and jaw sizes and relative molar development, while the second posits a relationship between relative molar development and the potential rapidity of skeletal maturation. As formulated here, both hypotheses assume that the differences in relative dental development found between the three specific samples in this study can be extrapolated to Europeans/European-Americans, black Africans, and Native Americans in general. We are aware that this remains to be established. However, for the purpose of generating potentially falsifiable hypotheses regarding the significance of population variability in relative dental development, this will be assumed.

Hypothesis #1. Bradley (1961), Brown (1978), Fanning (1962), Hunt (1959), Moorrees (1967), Odusanya and Abayomi (1991), and Stringer et al. (1990) have all argued that the timing of eruption is probably influenced by tooth-jaw size relationships. The apparently larger jaws of many African peoples (Aitchison, 1963; Merz et al., 1991) might also be a contributing factor to their pattern of relative M3 and M2 calcification. Stringer et al. in particular suggest that "... the large jaws and well-spaced teeth of many African blacks are likely to advance tooth emergence ..." (1990, p. 121).

In addition, third molar agenesis also appears to be related to jaw length. Anderson et al. (1975) found a significant negative correlation between maxillary length and agenesis of third molars (individuals with agenetic M3's had shorter maxillary lengths). Chagula (1960) has found a very low incidence of third molar agenesis in East African males (1.9%). Fanning (1962) noted that this figure was lower than that known for Europeans/European-Americans and Eskimos.

The first hypothesis proposes that an interplay between tooth and jaw sizes determines the relative and absolute timing of dental calcification and eruption, and the frequency of third molar agenesis. Populations characterized by jaws with more space for developing teeth should have advanced calcification and eruption schedules (relatively and absolutely) and lower frequencies of third molar agenesis compared to populations with more space restrictions.

With regard to this first hypothesis it must be noted that Garn et al. (1961, 1963) demonstrated a relationship between third molar agenesis and delayed calcification of other postcanine teeth. They suggest that agenesis might be one end of a spectrum in the expression of genetic factors responsible for delayed tooth formation. Since agenesis can be considered as the extreme of tooth size reduction, some of the differences between the groups in the present study could be partially the result of genetic differences in potential tooth size. There is some evidence to support this idea. Merz et al. (1991) concluded that the mesio-distal diameters of the mandibular canines, premolars and first molars in their African-American sample were statistically significantly larger than in their European-American sample. Nonetheless, this African-American sample did not show increased tooth crowding. Merz et al. (1991) concluded that the African-American sample achieved more than sufficient space for these larger teeth by means of greater dental arch widths and lengths than found in their European-American sample.

It may be that African-derived populations have, on average, both larger tooth dimensions *and* greater space for their developing teeth than European-derived populations. Thus relative molar development patterns may be due to a combination of two independent factors, tooth size and jaw size.

Hypothesis #2. There are several reports of advanced skeletal development in Africans and African-Americans compared to Europeans and European-Americans (Garn et al., 1972; Hiernaux, 1968; Malina and Little, 1981; Marshall et al., 1970; Massé and Hunt, 1963; Owen et al., 1974; Roche et al., 1975; Tanner, 1962). This advancement ranges from earlier median ages for first appearance of ossification centers in the wrist, hand, and lower limb to advanced "skeletal ages" for given chronological ages during childhood and the juvenile years. However, it is important to note that Africans and African-Americans are not necessarily the most advanced of all groups compared in these studies, and this advancement is most often not consistent throughout the entire growth period (Eveleth and Tanner, 1990; Marshall et al., 1970; Massé and Hunt, 1963; Roche et al., 1975, 1978). Also, there are reports of skeletal retardation in some African and African-derived samples compared to European and European-derived standards (Levine, 1972; Michaut et al., 1972). Southern Africans appear to be one of the African groups with relatively delayed skeletal development (Chertkow, 1980; Tobias, 1958).

From their broad review of the available literature, Eveleth and Tanner (1990) conclude that "... African children under good nutritional and environmental circumstances are more advanced than Europeans in skeletal development from birth until adolescence. There are no data showing whether the advancement continues into adolescence, though it seems probable" (1990, p. 155).[4] The retardation in skeletal development reported for some groups of African children are probably due, they argue, to a relative decline in nutrition and other environmental factors which prevent them from continuing to express their genetic potential for more rapid skeletal development. This is most likely the case for southern Africans, given the socioeconomic circumstances they have lived in during the latter part of this century.

The second hypothesis proposed here [based in part on ideas put forward in Fanning and Moorrees (1969) and Eveleth and Tanner (1976)] is that advanced relative M3 (and M2) development in one population versus another (Africans versus Europeans/European-Americans) is a genetic correlate of the potential for advanced skeletal development. (To phrase this hypothesis in a different, but equally appropriate manner, delayed relative molar development is a genetic correlate of the potential for less rapid skeletal development). Although the rate of skeletal development is more plastic than that of dental development (Garn et al., 1965a,b; Green, 1961; Lewis and Garn, 1960), the *potential* rates of development of these two hard tissue organ systems are probably linked genetically to a greater degree than some of the clinical literature based on phenotypic correlations suggests.

This proposed linkage does not mean that a close relationship exists between the two systems during adolescence. Later stages of M3 calcification and its eruption may not correlate with any skeletal maturation events in any population. The linkage between the two systems only concerns the timing of initial formation of the second and third molars and various ossification centers. Stated simply, it is proposed that there are differences between populations in genes operating during infancy and childhood which affect the timing (both relative and absolute) of beginning dental *and* skeletal formation.[5]

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[4]In the first edition of their book, Eveleth and Tanner (1976) were less cautious in their conclusions, stating that "... Afro-American children mature faster from birth onwards, alike in dental development, skeletal maturity, pubertal development ... and percentage of adult height attained at successive ages. There is little reason to suppose that groups of Africans in Africa would not grow similarly if their environmental conditions were better" (1976, p. 274).

[5]Fanning and Moorrees (1969) suggested something similar to this in their article on relative dental development in Australian aborigines and Caucasoids: "... Negro children, whether in America or Africa, are reported to be more advanced skeletally at birth than European children. Thus, earlier third molar emergence in Africans may be explained partially by the fact that at birth Negroes have reached a maturational stage that chronologically is attained later by Caucasoid children" (1969, p. 999).

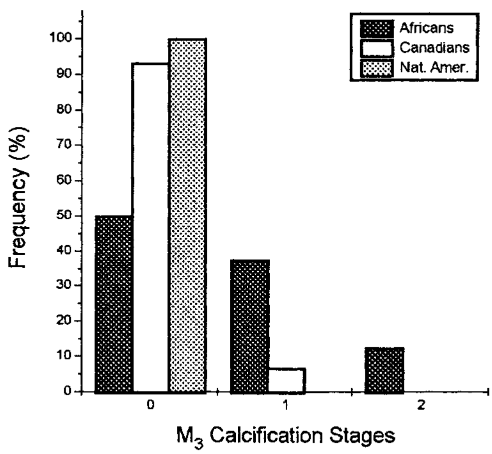

Fig. 13. Histogram of African, French-Canadian, and Native American M_3 calcification with M_1 at stage 10.

Figure 13 shows that even at the early stages of M3 development (using M1 as the reference tooth), the southern Africans are advanced over the French-Canadians. The vast majority of the French-Canadians (and Native Americans) show no radiographic trace of M3 formation, while half of the Africans have initiated the earliest stages of M3 formation. Thus advancement in relative M3 development in the Africans appears to be due largely to earlier initial formation of the tooth. Given the smaller amount of plasticity in dental formation, earlier initiation of M3 (and M2) development in the Africans leads to a fairly consistent advancement over the French-Canadians, while the more plastic nature of skeletal development means that, even with earlier appearance of certain ossification centers, skeletal development may not maintain its advancement throughout childhood and into the adolescent years in some African populations, particularly poorly nourished ones (Tanner, 1990).

While one or the other of these two hypotheses is the most likely explanation for population variability in relative molar development, it must be noted that an interplay of various factors is undoubtedly involved in relative dental development variability. In addition to the factors discussed above, the rate of wear on the teeth, and the level of circulating hormones related to sexual maturity are all thought to effect the timing of eruption (Begg, 1954; Bradley, 1961; Brown, 1978; Chagula, 1960; Fanning, 1962; Garn et al., 1965a; Hunt, 1959; McCullagh and Resch, 1941; Moorrees, 1967; Odusanya and Abayomi, 1991), and some of these same factors may also affect calcification patterns of successively forming teeth.

CONCLUSIONS

There are differences in the relative dental development of certain permanent teeth between black southern Africans, French-Canadians and Native Americans, specifically the markedly advanced calcification of the M_3 in the Africans relative to French-Canadians, the varying patterns of African and Native American advancement over the French-Canadians in M_2 calcification, and the advanced calcification of the canines in female French-Canadians. The results of this study correlate with and provide confirmation of the conclusions from several other studies on dental eruption and calcification in African-derived, European-derived, and Native American populations. More importantly, the results of the present study demonstrate that population differences in dental eruption and calcification schedules are due in part to differing patterns of relative development between teeth. Such differences undoubtedly contribute to the later ages of eruption reported for European-Americans versus Africans.

Two general hypotheses can be formulated concerning the significance of population differences in relative dental development. The first posits a relationship between tooth and jaw sizes and the timing of calcification and third molar agenesis, while the second proposes that the relatively advanced posterior molar development of southern Africans compared to French-Canadians is an indicator of their potential for more rapid skeletal development compared to French-Canadians and European-derived populations in general. These hypotheses are potentially falsifiable using appropriate data from living and skeletal samples of African and European/European-American subadults.

This research provides a solid basis for comparing fossil hominid patterns of relative dental development to the range of variability in modern humans. Such compari-

sons can help us to better understand not only the evolution of the human pattern of dental development, but the human pattern of growth and development in general.

ACKNOWLEDGMENTS

I thank Prof. C.B. Preston and Dr. M. Barter (University of the Witwatersrand), Dr. Verwyen and Prof. A. Ferreira (Medical University of South Africa), E.T. Maganu and the Ministry of Health of Botswana, Dr. A. Demirjian (Université de Montréal), Dr. Mary Powell (University of Kentucky), Dr. Frank Norick and Dr. Gary Richards (Hearst Museum, U.C. Berkeley), and Dr. Stanley Rhine and the Maxwell Museum of Anthropology (University of New Mexico) for permission to utilize the dental X-ray and skeletal collections which provided the data for this research. A big thanks to Prof. and Mrs. W. Evans of Johannesburg for their incredible assistance and hospitality. Dr. Steve Wagner of Albuquerque provided help with the early phases of this research. Drs. E. Trinkaus, B.H. Smith, J. Long, J. Lancaster, and J. Chisholm gave me valuable advice and support as members of my dissertation committee. B. Holly Smith, E. Trinkaus, R. Franciscus, T. Holliday, L. Winkler, R. Anemone, and three anonymous reviewers provided very useful criticisms of earlier versions of this paper. This research was supported by grants from NSF (BNS-8918011), the L.S.B. Leakey Foundation, Sigma Xi, and SRAC of the University of New Mexico.

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APPENDIX A: PREHISTORIC NATIVE AMERICAN SITES FROM WHICH IMMATURE INDIVIDUALS WERE DRAWN

In the eastern U.S. (University of Kentucky):

Carlston Annis (15-Bt-5)
Indian Knoll (15-Oh-2)
Chiggersville (15-Oh-1)
Reed Site (15-Bt-10)
Butterfeld Site (15-Mcl-7)
Cypress Creek/Ward Site (15-Mcl-11)
Hardin Village (15-GP-22)

In the southwestern U.S. (Maxwell Museum, University of New Mexico):

Pottery Mound
Mimbres
Kuaua
Sapawe
Pueblo Canyon Cliffs (Los Alamos Archaeological Society)

In California (Phoebe Hearst Museum, University of California at Berkeley):

The individuals utilized in the Hearst Museum collections come from a large number of different sites; the vast majority come from sites within California proper, but a few are from Pershing County, Nevada; the California sites are located in several different counties within California.

APPENDIX B

The Demirjian system uses the letters A–H to denote eight stages of tooth calcification, with a zero (0) assigned if there is no sign of calcification. The equivalence between the scoring system used in the present study and the Demirjian system is shown below. On the left under STAGES are three columns of numeric and alphabetic stages. The column on the far left lists the numeric stages utilized in the present study for incisors, canines and premolars. The middle column lists the numeric stages utilized for molars. The third column indicates the equivalence with stages used in the Dermirjian system. Descriptions of the modifications and additional stages used for the present study are explained with reference to the eight original stages in Demrijian et al. (1973). In the descriptions below, S is used as an abbreviation for the stages used in the present study, i.e., S3 = stage 3.

STAGES			DESCRIPTION
0	0	0	
1	1	A	
2	2	B	
3	3	C	
4	4		Stage C was divided into two halves, S3 and S4. S3 encompasses completion of enamel formation at the occulsal level up to, but not including, half crown complete. S3 fulfills Demirjian criteria a and b for their stage C. S4 encompasses the second half of crown development from half crown complete up to, but not including, crown complete/no root formation.
5	5	D	S5 encompasses crown formation complete down to the cemento-enamel junction up to, but not including, the beginning of root formation.
6	6		S6 is that stage where Demirjian criterion c of stage D (presence of a root spicule) is met.
7	7	E	For molars, the first of the two criteria used for Demirjian stage E was omitted ("initial formation of the radicular bifurcation is seen in the form of either a calcified point or a semi-lunar shape"). This was done because of variability in time of appearance of the bifurcation that occurs with taurodontism.[1] Any tooth with the bifurcation beginning to appear was placed at no less than S7. Root length is still less than crown height, but is now more than just a spicule.
8			This stage was added for incisors, canines, and premolars. It encompasses the period where root length is approximately equal to, but not obviously greater than, crown height. A tooth in this stage could satisfy the *shape* criteria for either stage E or F, as these shape criteria did not have a very consistent relationship with root length. This stage would be collapsed into stage F.
9	8	F	Uniradicular teeth: In the present study this stage was assigned to those teeth fulfilling criterion (a) for Demirjian stage F but with root lengths *greater* than the crown height. Molars: Root length is equal to or a little greater than crown height. Demirjian criterion (a) for stage F was used as a secondary criterion, because extremely taurodont molars may not show the bifurcation even with this much root formed.[2]

(continues)

APPENDIX B *(continued)*

STAGES			DESCRIPTION
10	9		Uniradicular teeth: the root canal walls are now parallel except at the root apex where a funnel shape is still evident. Molars: root length is notably greater than crown height, but is less than 75% of the projected root length. The criterion for uniradicular teeth served as a secondary criterion for molars.[3] In the case of molars this stage would be collapsed into stage F; for all other teeth it would be collapsed into stage G.
	10		This stage was interpolated solely for molars. Root length is at least 75% of its projected length, but the criteria for stage G are not met. Root canal walls are now parallel with no obvious funnel shape at the apices (at most a very slight funnel shape), but the apical aspects of the root walls are thicker than at stage G. This stage would be collapsed into stage G.
11	11	G	For molars an added criterion was that the apical aspects of the root walls do not appear as thick as in stage 10 and the root tips have a distinctly pointed appearance. Root length is nearly complete (well beyond 75% of its projected length).
12	12		This last interpolated stage applies to all tooth types. It is a division of stage G and would be collapsed back into that stage. S12 refers to teeth with the root canal walls much more narrow than at stage G, but definitely not yet at stage H. It is equivalent to the Moorrees et al. (1963) stage Apex $\frac{1}{2}$.
13	13	H	

While some of the above additions and modifications correspond exactly to stages in the Moorrees et al. (1963) system, this is not true for all of them. Stages 3 and 4 correspond to the stages denoted $Cr\frac{1}{2}$ and $Cr\frac{3}{4}$, respectively, in the Moorrees et al. system. Stages 5 and 6 correspond to the Moorrees stages Cr_c and R_i, and stages 11 and 12 correspond to the Moorrees stages R_c and $A\frac{1}{2}$. The other modifications utilized here do not correspond precisely to any of their categories.

[1-3]Various degrees of taurdontism were found in low frequencies among all the recent human samples. It is found in much higher frequencies and is expressed more extremely among Upper Pleistocene hominids. As the recent human data was collected for the purposes of comparison with Upper Pleistocene hominid samples, it was necessary to make changes to the Demirjian et al. system with regard to cleft appearance and root bifurcation. However, for the vast majority of the recent humans (and for most fossil hominids), the criteria based on root bifurcation changes were applicable and the order of criteria used by Demirjian et al. (1973) would have been appropriate.